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STUDIES IN THE GRAMINEAE.

VIII. MUNROA SQUARROSA (NUTT.) TORR.[1]

THEO. HOLM.

(WITH TWELVE FIGURES)

IT often happens that plants which are common and easily available are the least studied. Being frequently collected and represented in herbaria by almost numberless specimens, such plants become so familiar "by name" that botanists as a rule do not take the pains to examine them with much interest or care.

The steady increase in the publication of cheap systematic works in this country is hardly beneficial to the study of taxonomic botany. The danger lies in the fact that authors of such works seldom take the time to reexamine the plants or to compare them with diagnoses of earlier date. It is no surprise, therefore, to discover points of great importance mentioned in earlier diagnoses which have been totally overlooked or ignored in works of a more recent date. As a matter of fact, the older botanists were more careful in examining and describing their plants, and their diagnoses, brief as they may be, often allude to certain characters which are well worthy of notice. A case in point may be illustrated by Munroa, and in selecting this genus as the subject of the present paper, it is with the intention of showing that the plant was actually better understood formerly than it is now, and that it possesses certain morphological and histological characters which have not been observed hitherto and which may be of some importance to future research.

Munroa was first described as a species of Crypsis—*C. squarrosa*—by NUTTALL, but TORREY corrected the mistake and established the genus.[2] At that time it was considered as belonging to the HORDEAE, while it is now generally placed among the FESTUCEAE. As described by TORREY, the plant is readily recognized, and both the singular habit and the inflorescence are exceedingly well characterized. There is one point especially which has escaped the attention of later botanists, namely, that the spikelets are dimorphic in respect to the shape of the glumes. It is true that TORREY did not express this as plainly as he might have done, but his diagnosis certainly shows that he did observe the different structure of the spikelets, as shown by the following statement: "In the uppermost spikelet, and often in the middle one, these nerves are bearded with long white hairs towards the base; but the flowers of the lowest spikelet are usually quite naked." That BENTHAM and HOOKER considered this character of some importance is evident from their description of the flowering glumes as being "longe ciliatis v. in eodem fasciculo glabris."[3] But none of the subsequent authors, not even the agrostologists, appear to have noticed this point, and it so happens that the genus has been received as a plant of rather ordinary habit, distinct from Monanthochloe by "Spikelets usually in threes, terminal in the axils of stiff spinescent leaves which project far beyond them."[4]

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[1] Earlier papers were published in this journal as follows: I, June 1891; II, August, 1891; III, October 1891; IV, November 1892; V, August 1895; VI, June 1896; VII, November 1896.

[2] Pacific R. R. Rep. 4:158. 1856.

Since TORREY called attention to this slight modification in structure of the flowering glumes, it seemed natural to investigate the matter further, as it might lead to the discovery of additional characters sufficient to attribute a certain degree of dimorphism to the spikelets. A careful examination of a large number of specimens, studied in the field, revealed the fact that Munroa does exhibit such dimorphism constantly, and to a greater extent than hitherto observed. The deviation is not only due to the presence of long white hairs at the base of the flowering glume in the uppermost spikelet in contrast with the others, as first described, but the complete structure of these spikelets is quite prominently distinct. As a rule, each inflorescence (*fig. 1*) in Munroa consists mostly of three spikelets, one median and two lateral; and when only two are developed, one of them shows always the structure of a median and the other that of a lateral spikelet. Of the two spikelets here figured, *fig. 2* represents the median and *fig. 3* one of the two lateral. It is readily seen from the drawings that the structure of these spikelets is distinct. The empty glumes are very unequal (*figs. 2* and *4*) in the median, but almost equal in the lateral spikelets (*fig. 3*); the flowering glume is pubescent in both, but in the median there are three distinct nerves with a tuft of long hairs at the base (*figs. 2, 5*, and *6*), while in the lateral the nerves are not visible, and no long hairs are developed (*figs. 3* and *7*); moreover, the apex of the flowering glume is long-awned and distinctly bidentate in the median (*figs. 5* and *6*), but merely emarginate and short-awned in the lateral spikelets (*fig. 7*). Some distinction in regard to texture is also observable, the flowering glume and the palet being membranaceous in the median, but quite thick and coriaceous in the lateral spikelets. It may seem justifiable, therefore, to consider the spikelets of Munroa as being dimorphic, even if we have not been able to observe any deviation in regard to the distribution of the sexes within them.

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[3] Genera plantarum **3**:1180. 1883.

[4] SCRIBNER and SOUTHWORTH, The true grasses. New York. 137. 1890.

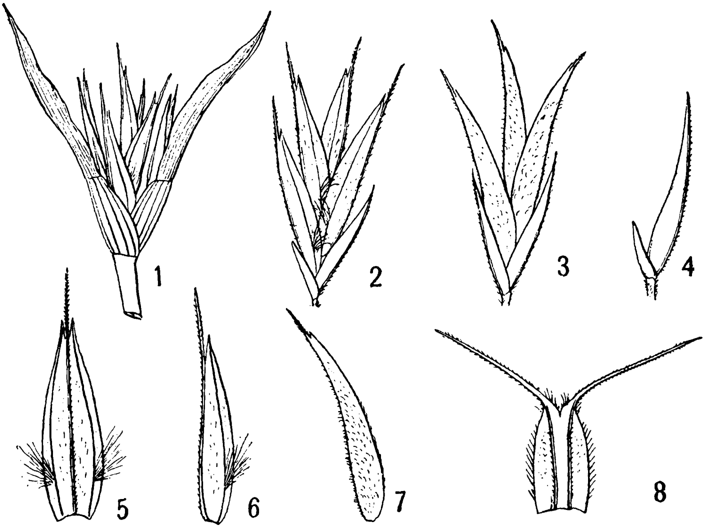

FIG. 1.—*Munroa squarrosa*.—The inflorescence, magnified. FIG. 2.—A terminal spikelet. FIG. 3.—A lateral spikelet. FIG. 4.—The empty glumes of a terminal spikelet. FIG. 5.—Flowering glume of same, dorsal view. FIG. 6.—Same, side view. FIG. 7.—Flowering glume of lateral spikelet, side view. FIG. 8.—The prophyllon, dorsal view.

While TORREY'S description of the spikelets contains a good deal more than is recorded by subsequent writers, except BENTHAM and HOOKER, there are some other points which may be added to the diagnosis of this singular grass. The mode of growth is very well characterized by TORREY, but there are some peculiarities which have been omitted, and these consist especially in the structure of the shoots, the vegetative and the floral; furthermore, the histology has only been touched upon very briefly.

The peculiar bushy habit of the plant depends upon the fact that the culms are not directly terminated by the inflorescence. Usually in the Gramineae the long internode of the culm passes immediately over into the inflorescence, but in Munroa the spikelets are preceded by two or three green leaves which are borne upon the culm near the apex, and whose internodes are exceedingly short, often being barely visible. These green leaves all subtend shoots, which develop into floral or vegetative branches, and quite often into secondary culms from the apex of which the same development of shoots is repeated. Beneath the terminal inflorescence there is thus a small cluster of shoots, developed in the axils of green leaves, a ramification that calls to mind the well-known condition known in teratology as "prolification," but which is normal and constant in Munroa. To separate these shoots and to define their proper order might at first glance seem difficult, not only on account of their relatively large number, but also because the internodes are so very short. However, if we examine the shoots carefully, it is easily seen that the first leaf of several of them represents a fore-leaf (prophyllon) of most characteristic and striking shape.[5] The presence of a fore-leaf actually gives the clue to the composition of these "fascicles of leaves and shoots," since it always signifies a lateral ramification, and in the Gramineae is nearly always situated on the branch with its dorsal surface toward the mother axis. In Munroa this prophyllon has attained a high development, and is not only represented by an open sheath-like body, but the two nerves are extended into very long, stiff, divergent setae (*fig. 8*); the sheath-like portion is membranaceous, ciliate, and minutely pubescent on the dorsal face. Altogether it is a structure so remarkable and characteristic that it may well deserve to be mentioned in the diagnosis of the genus.

The composition of the shoots in Munroa is illustrated by the two accompanying diagrams (*figs. 9* and *10*), which represent two frequent instances of ramification. In these diagrams L^1, L^2, etc., all represent assimilating leaves with sheaths and blades developed as ordinary grass leaves, and they differ in no respect from the others which are situated at the base of the culms, where they form a dense rosette. On the other hand, P^1, P^2, etc., are prophylla or fore-leaves, and their form as indicated is almost like their cross-section. Thus their actual position may be readily understood, the concave side (dorsal) turning toward the mother axis. S^1, S^2, etc., are the spikelets, of which only the empty glumes and one of the flowering have been drawn, in order to show the mutual position of the spikelets—median and lateral—and of their respective glumes.

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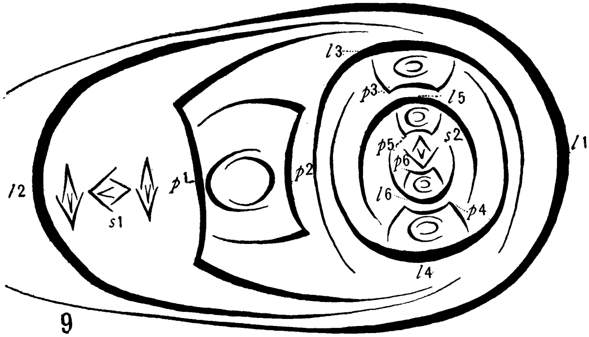
[5] Some new anatomical characters for certain Gramineae. Beihefte Bot. Cent. **11**:28. 1901.



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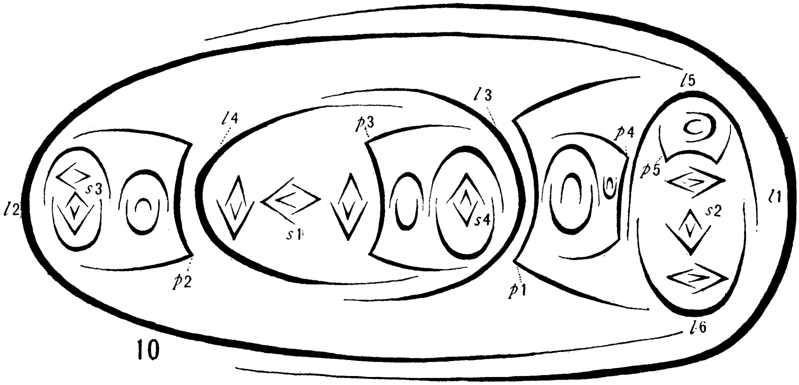

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FIGS. 9 and 10.—*Munroa squarrosa*. Diagrams of two fascicles of shoots from the apex of two culms: *l*, the green leaves; *p*, the fore-leaves; *s*, the spikelets; for further explanation see text.

In *fig. 9* the two leaves L^1 and L^2 are developed a very short distance below the inflorescence (S^1), which terminates the culm of the main stem; they are exactly alternate, and so are the glumes of the median spikelet (S^1); in the two lateral the same position is noticeable, but these have been turned so as to form an angle of 90° with the median, the terminal spikelet. In the axil of L^1 a complex of shoots may be seen, beginning with a prophyllon (P^1) with its back toward the main axis, but alternating with the leaf L^1. The subsequent leaves (L^3–L^6) of this axillary shoot, on the other hand, are turned 90° to the side of the leaf L^1, but are otherwise alternate. The first of these leaves (L^3) supports a bud with a prophyllon and two small leaves, and similar buds are also observable in the axils of the other leaves (L^4–L^6). The apex of the whole shoot terminates in a single spikelet (S^2), the arrangement of whose glumes, alternating with the green leaves of the same axis, shows that it is a median and not one of the lateral spikelets; these have become suppressed entirely in this instance.

There is still another shoot observable, however, namely the one whose prophyllon is marked P^2, and which has only two green leaves. This little shoot comes from the axil of the large prophyllon P^1, Munroa thus illustrating a case, not unusual among Gramineae, in which prophylla may subtend shoots. It is furthermore noticeable that this prophyllon (P^2) and the leaves of its shoot lie distinctly in the same plane as the first leaves (L^1 and L^2) and the first prophyllon (P^1). In this way the spikelet S^1 terminates the main culm, while the other (S^2) terminates the shoot developed from the axil of the leaf L^1.

The succession of these various leaves (L and P) seems invariably the same, inasmuch as no instance was observed where the inflorescence was directly preceded by a prophyllon alone. But the number of vegetative shoots in Munroa is sometimes much larger than that of the floral, and the reason seems to be, at least judging from this particular instance (*fig. 9*), that the shoots were so crowded within the leaf axil that the development of flowers became arrested. This explanation may seem justifiable when we examine the other diagram (*fig. 10*), which shows a more balanced growth of the whole system of axes, instead of the one-sided development of shoots shown in the former diagram (*fig. 9*), where no axillary branch was developed from the leaf L^2, but only from L^1.

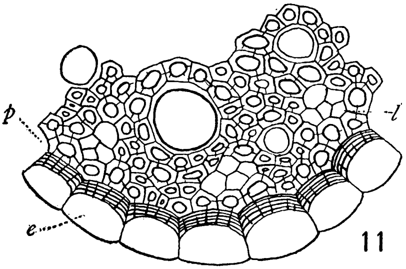
In *fig. 10* there are represented four inflorescences and five vegetative shoots, but much more equally distributed than before, since the main culm bears here a larger number of leaves—four instead of two—three of which (L^1–L^3) subtend shoots. These leaves (L^1–L^4) are also exactly alternate and lie in one plane, and the uppermost (L^4) precedes an inflorescence (S^1) which terminates the main culm. Similar to the specimen illustrated in *fig. 9*, the first leaf (L^1) subtends a shoot with a large prophyllon (P^1), and this shoot is also turned 90° to the side of the supporting leaf and the prophyllon; but it bears only two leaves (L^5 and L^6), one of which (L^5) has an axillary shoot consisting of a prophyllon and a vegetative apex. The other leaf (L^6) has no shoot and precedes the terminal inflorescence (S^2) of three spikelets, arranged in conformity with the leaves (L^5 and L^6). Another shoot is observable in the axil of the large prophyllon P^1, which shows the same development as the one in *fig. 9*, but with the exception that an axillary shoot is visible within the prophyllon (P^4); thus two prophylla of the shoot-complex pertaining to leaf L^1 support buds.

Examining the other shoots, we find one in the axil of leaf L^2 with a prophyllon (P^2), whose leaves and inflorescence are likewise turned 90° to the side, with exception of the prophyllon. This shoot consists of a terminal portion with two leaves and a two-flowered inflorescence (S^3; one median and one lateral spikelet), besides a secondary, purely vegetative bud which is developed in the axil of the prophyllon, but although axillary its prophyllon has become suppressed. The position of the floral shoot, however, shows clearly that it is terminal, and that the other much smaller one must belong to the prophyllon. A similar construction of two shoots pertaining to one system is to be found in the axil of the leaf L^3, where we observe the same position of the prophyllon (P^3) and of the green leaves as before. The shoot bears two leaves and is terminated by a single spikelet (S^4), which shows the arrangement of the glumes as that of a median rather than of a lateral spikelet, since the glumes alternate with the leaves. It is now interesting to see that the prophyllon (P^3) here also subtends a bud, and a purely vegetative one. The fourth leaf (L^4) has no bud and precedes directly the inflorescence (S^1), which terminates the main culm; thus the median spikelet represents the uppermost terminus, and its glumes are situated so as to alternate with the four leaves (L^1–L^4) borne on the culm.

Such is the usual composition of the fasciculate shoots in *Munroa squarrosa,* but there are of course many variations in proportion to the number of shoots developed. However, the succession of leaves appears constant, and the modification by suppression of some of the spikelets or of the vegetative shoots does not influence the principal structure as described above. It is a structure which no doubt is uncommon among the Gramineae, even if the components of the shoots may be identical. Somewhat similar and equally complicated cases of ramification may be observed in Coix, in Andropogon, and especially in Jouvea. North American Gramineae exhibit altogether a number of types in regard to inflorescence and ramification of axes which are very little known and which deserve attention. In Munroa the most striking peculiarity depends, as stated above, upon the presence of short internodes with green leaves above the longest internode of the culm, preceding the terminal inflorescence. Furthermore, it is characterized by the profuse development of shoots, floral and vegetative, from the axils of these leaves; and also by the elongation of some of these into secondary culms, at the apex of which the same development of fasciculate shoots occurs.

From a morphological aspect, therefore, *Munroa squarrosa* offers several important characters, but it exhibits also some points of histological interest, which may be mentioned in this connection. As an inhabitant of the arid plains, it would be expected that our plant would possess a xerophytic structure, which it does; but such structure is far from common among its associates. Ecological studies are very seldom extended beyond the mere fact that such and such plants constitute associations; whether the external and internal structure of such xerophytes, for instance, is in real harmony with the surroundings is very seldom touched upon. The xerophytic characters have been very excellently defined by several prominent authors, by WARMING and SCHIMPER for instance; but whether these characters are to be observed in all the members of such xerophilous associations remains to be seen. It would require an immense amount of work, and nothing more or less than a complete investigation of the internal structure of desert plants. Very few of our plants have been studied from this particular point of view, and the following notes on the histology of *Munroa squarrosa* may be regarded, therefore, as a small contribution towards the knowledge of this interesting plant association. With this object in view, the writer has examined the structure of the roots, the culm, the proper leaves, and the prophyllon, and finally the flowering glumes of both forms of spikelets.

THE ROOTS.—The roots are thin, hairy, not very strong, relatively short, and but little ramified. In a mature root the epidermis and the moderately thick-walled hypoderm persist, but the cortex, which consists of only three or four layers, collapses radially. The inner walls of the endodermis (*fig. 11, e*) are considerably thickened with distinct layers and pores; and it surrounds a pericambium which is thickened throughout. Therefore the location of the proto-hadrome vessels could not be clearly ascertained, and the inner portion of the central cylinder is occupied by a mass of thick-walled conjunctive tissue with about ten broad rays of hadrome. The leptome constitutes very small groups, when viewed in transverse sections (*fig. 11, l*). A younger stage of the root shows these same elements much less thick-walled. Thus it was possible to distinguish the pericambium cells from the proto-hadrome vessels, and it was noticed that the latter had penetrated the pericambium in all places. If one of the capillary lateral roots (*fig. 12*) is examined the same structure is observed, but the center of the root is here occupied by a large vessel, and the hadromatic rays are merely represented by four proto-hadrome vessels (*fig. 12, h*), all of which are located inside the peri-



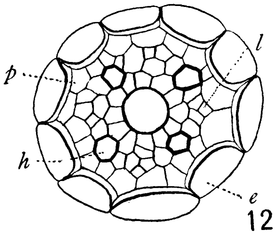


FIG. 11.—*Munroa squarrosa.*—Transverse section of a mature root: *e*, endodermis; *p*, pericambium; *l*, leptome. X 560. FIG. 12.—Transverse section of a capillary lateral root: *h*, proto-hadrome; the other letters as above. X 560.

cambium. We do not attach much importance to this varied position of the proto-hadrome, however, since we have ascertained that it is not constant, a fact that has been recorded in some previously published papers.[6] A characteristic of the root of Munroa seems to be the poorly developed cortex in contrast with the prominent and thick-walled inner tissues of the central cylinder.

THE CULM.—The long internode is semicylindric, smooth, and almost glabrous at the base; but cylindric, deeply furrowed, and scabrous above. The smooth and quite thick cuticle covers a very small-celled epidermis, whose outer walls are prominently thickened. Stomata are frequently near the furrows of the upper part of the culm, and their guard cells are level with the epidermis. Unicellular, pointed projections abound along the elevated ridges, but decrease in number toward the base, where the surface of the culm is smooth. The cortical parenchyma is well differentiated in the upper part, where it occurs as a single layer of palisade cells, filled with chlorophyll, and bordering on the parenchyma sheath of the peripheral mestome bundles; the palisades are very regularly arranged, radiating from the parenchyma sheath. Another tissue of about five layers, but composed of colorless, more roundish cells, occupies the space between the peripheral mestome bundles with their covering of palisades, and this tissue belongs also to the cortex. It is developed to a somewhat larger extent at the base of the culm, where no palisades were observed; thus the cortex consists here of a continuous ring of colorless tissue surrounding the mestome bundles.

The mechanical tissue as stereome is well represented and forms sub-epidermal groups in the ridges, bordering on the palisades, besides occurring as a solid, continuous zone all around the inner mestome bundles. Toward the base of the culm the stereome does not occur as sub-epidermal layers, but only as a heavy ring inside the cortex and surrounding both the outer and inner circle of mestome bundles. Throughout the culm there are thus two almost concentric circles of mestome bundles, the peripheral ones being the smaller, orbicular in transverse section, and containing mostly leptome alone; while the larger inner ones are oval and contain both leptome and hadrome. Common to both is a thick-walled mestome sheath, but the parenchyma sheath is developed only on the outer face of the peripheral bundles, thus bordering on the palisades, being quite large-celled and containing chlorophyll of a somewhat bluish-green color. This parenchyma sheath is thus restricted to this particular portion of the peripheral mestome bundles in the upper part of the culm, where palisades occur, and is entirely absent in all the others. The inner portion of the culm is occupied by a thin-walled pith, which is broken in the center.

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[6] Compare: *Eriocaulon decangulare* L. BOT. GAZETTE **31**:17. 1901; and Studies in the Cyperaceae. XIV. Amer. Jour. Sci. **10**:278. 1900.

Characteristic features of the culm, therefore, are the small development of chlorophyll-bearing parenchyma in the shape of palisades and as an incomplete parenchyma sheath, and the predominating chlorophyll-less cortical parenchyma which evidently has the function of storing water. The stereome is well represented, being thick-walled and constituting heavy layers both in the ridges and inside the cortex.

THE LEAF.—The leaf blade is furrowed on both faces, deepest on the ventral, and covered with small obtuse papillae and somewhat larger prickle-like projections like those observed on the culm. The midrib is hardly larger than the other nerves, the blade thus being nearly flat and of the same thickness throughout. Stomata occur on both faces of the blade along the sides of the furrows, their guard cells being level with epidermis. While the cells of epidermis are small and quite thick-walled on the dorsal face of the leaf, those of the ventral are larger and developed as bulliform cells in the furrows between the mestome bundles.

The parenchymatic tissues of the leaf consist of a colorless water-storage tissue, which is located in the furrows beneath the bulliform cells, and consisting of three or four strata. There is also a chlorophyll-bearing tissue, developed as one layer of palisades surrounding the mestome bundles and radiating from them. Similar palisade cells were also noticeable in the upper portion of the culm, and bordering on the incomplete parenchyma sheath.

The mestome bundles are all orbicular in transverse section, and possess a complete green parenchyma sheath besides a mestome sheath, which is somewhat thick-walled in the larger bundles. The leptome and hadrome are well differentiated in all the nerves, especially in the larger ones. In regard to the mechanical tissue, a stereome occurs in large groups, one in each margin of the blade, besides smaller groups accompanying the nerves, and located above and below them between epidermis and palisades.

Characteristic of Munroa and several of its associates among the Gramineae are the nearly orbicular mestome bundles surrounded by the single layer of straight-walled palisades, radiating from them and bordering on a rather large-celled parenchyma sheath, inside of which a typical mestome sheath occurs; and also the deeply furrowed blade with bands of bulliform cells covering strata of colorless tissue, the function of which is evidently to store water. The numerous epidermal projections in the shape of papillae or long-pointed spines partly surround and cover the stomata.

THE PROPHYLLON.—This very characteristic leaf, as stated above, consists of a sheath-like, bicarinate, membranaceous body and two long setae, the nerves being extended beyond the apex of the leaf. The structure of the sheath-like portion is very simple, since the margins and the central part possess only an epidermis (the dorsal) with a few stereomatic cells scattered here and there. The two keels, in which two mestome bundles are located, show a more solid structure, since each keel has a support of quite thick-walled stereome, which borders on a large-celled, colorless parenchyma. Each mestome bundle has a closed parenchyma sheath and a moderately thickened mestome sheath. The awns contain chlorophyll, located in a stratum of palisades and in the parenchyma sheath, and stomata occur on the upper surface. A cross-section of one of these awns is sharply triangular, with the two lateral angles occupied by stereome, while the keel contains a large mass of colorless parenchyma. The mestome bundle is located in the center, but is very small and consists only of leptome.

THE FLOWERING GLUMES AND THE PALETS.—As stated above, the glumes of the terminal spikelet are somewhat different from those of the lateral in regard to shape and texture, and therefore the spikelets may be designated as "dimorphic." This distinction, however, seems much more pronounced when the internal structure is compared. The empty glumes of both spikelets possess the same structure, even if their form be distinct; but the flowering glumes and the palets exhibit a structure so distinct that when detached the spikelets may be easily assorted into terminal or lateral by their tissues alone. In the terminal spikelet the flowering glume and the palet are thin and membranaceous, as in the majority of Gramineae. The flowering glume has four prominent ribs on the dorsal face supported by heavy groups of stereome, and small scattered groups of this same tissue are observable also on the ventral face of the glume, but only between the two innermost mestome bundles. Otherwise the glume consists only of a single layer throughout, represented by the dorsal epidermis. The palet of this same spikelet—the terminal—is two-nerved, but very slightly bicarinate, and the structure is even more delicate than that of the flowering glume.

In the flowering glume of the lateral spikelets the structure is very different, a large mass of very thick-walled stereome covering nearly the whole ventral face of the glume, and a colorless parenchyma occupying the larger inner portion. The four mestome bundles are imbedded in this tissue, thus forming no prominent ribs, as is the case in the terminal spikelet. A similar broad stereomatic tissue is observable in the palet on the ventral face, besides a colorless tissue nearer the dorsal. The two nerves are located in this tissue, which extends into two sharp keels with numerous epidermal projections.

So great a diversity in structure observable in the glumes of spikelets belonging to the same inflorescence is evidently very rare within the order. It seems the more peculiar since the spikelets are otherwise identical, the number of glumes being the same, and the flowers perfect in both the terminal and lateral spikelets. The very firm structure, described above, which is especially marked by the unusual development of stereome, is also known in other genera. We might mention, for instance, the coriaceous or cartilaginous empty glumes in MAYDEAE and ZOYSIEAE; the cartilaginous flowering glume and palet in PANICEAE and ORYZEAE; finally the prominent structural deviation noticeable in the unisexual spikelets of Buchloe and Amphicarpum. But none of these cases are really comparable with that of Munroa, where the only distinction between the spikelets depends upon position, terminal or lateral, and not upon the distribution of sexes, and still exhibiting such marked modification in structure.

The systematic position of Munroa seems naturally to be within FESTUCEAE, but it is difficult to place it near any of the genera so as to demonstrate its nearest affinity. Most frequently Munroa is placed next to Monanthochloe, a genus to which it certainly shows no affinities whatsoever. The peculiarity of the genus seems to depend upon the dimorphism of the spikelets, and to some extent upon the profuse development of shoots, especially vegetative, in the axils of leaves near the apex of the culm, a structure which is exceedingly common in teratological cases, but which is normal and constant in *Munroa squarrosa.*

There may exist some analogous cases, and normally so, among the other members of the order in this country, but so far as known to the writer no investigations have been published dealing with such morphological peculiarities.

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